



Aquatic communities in arid landscapes: local conditions, dispersal traits and landscape configuration determine local biodiversity

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ABSTRACT

Aim To understand how environmental conditions and landscape structure interact at different spatial scales to shape the community composition of arid zone aquatic invertebrates with different dispersal abilities.

Location Australia.

Methods For each of five drainage basins and for their encompassing region (Pilbara), we built matrices of dissimilarities in presence–absence patterns of aquatic invertebrate community composition. This was carried out for all taxa collectively and separately for five dispersal trait groups: obligate aquatics, passive aerial dispersers, animals moving by aerial phoresy, weak and strong fliers. We analysed correlations between community dissimilarities and (1) dissimilarities in local environmental conditions, (2) geographic distances and (3) landscape resistance distances among the sites from which invertebrates were sampled. Calculation of landscape resistances accounted for longitudinal connectivity along the river channels (least-cost-path), lateral connectivity between streams and the potential effects of rugged topography on invertebrate dispersal.

Results Local environmental factors and landscape resistances explained differences in community composition at the regional scale. In basins with complex topography, local environmental conditions were the main factor explaining community dissimilarities in most dispersal groups. Conversely, in basins where flatter topography meant that moderate to high lateral connectivity between streams is possible, the spatial configuration of the dendritic network determined the community composition of most dispersal trait groups. Geographic and least-cost-path distances were poor predictors of community composition. None of the groups showed a consistent correlation with environmental factors alone, or just landscape resistances, across all basins.

Main conclusions Local environmental conditions, hydrological connectivity and landscape resistance to dispersal are all important influences on community composition of arid zone aquatic invertebrates. The impact of each of these factors varies with dispersal trait group and spatial configuration of basins: the importance of lateral connectivity for explaining a substantial proportion of community composition points to a major role of flooding regimes in maintaining biological communities.

Keywords

CIRCUITSCAPE, community structure, functional connectivity, Mantel tests, resistance distance, river networks.

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INTRODUCTION

Composition of ecological communities can be shaped by the interaction of three non-exclusive factors: local ecological conditions (biotic and abiotic), context and spatial configuration of the landscape (e.g. distribution of habitats, topographic barriers and corridors) and dispersal abilities (Tilman, 1982; Hubbell, 2001; Chave, 2004; Leibold *et al.*, 2004; He *et al.*, 2005; Heino, 2011). The importance of these three factors in spatial structuring of communities may differ depending on environmental heterogeneity and spatial scale (Leibold *et al.*, 2004; Heino, 2011; Moritz *et al.*, 2013). For example, dispersal limitation tends to exert a stronger influence on patterns of community composition at larger scales, whereas ecological factors may be more influential at local scales (Heino *et al.*, 2012). Understanding the processes through which these factors structure communities is important for predicting community responses to a range of impacts, including habitat fragmentation and climate change (Brown *et al.*, 2011). This understanding can be improved by analysing distance–decay relationships between pairwise community dissimilarities and (1) geographic distances (Beisner *et al.*, 2006; Thompson & Townsend, 2006; Astorga *et al.*, 2012), (2) distances along assumed dispersal routes (Brown & Swan, 2010) and (3) differences in environmental conditions (Nekola & White, 1999). The lack of consistent patterns in relationships between community dissimilarities and these three potential drivers across studies (e.g. Thompson & Townsend, 2006; Heino, 2011) suggests that there is a need to understand the processes which underpin these patterns in a more sophisticated way. When performed for taxa grouped by dispersal traits, analyses of distance–decay relationships may reveal the effect of dispersal ability on community dissimilarity (Thompson & Townsend, 2006).

Arid zone riverine ecosystems are excellent model systems for studying the interactive effects of environment, landscape and dispersal on community structure. Arid zone aquatic habitats contrast strongly with the hostile intervening matrix so that habitat elements are relatively discrete and measurable; they have diverse communities displaying a range of dispersal traits, and environmental parameters can be measured in standardized ways (Sheldon & Thoms, 2006; Pinder *et al.*, 2010). Accordingly, in this study, we analysed the effect of local environmental conditions, geographic distance, landscape configuration and organismal dispersal abilities on community composition of aquatic invertebrates from the Pilbara, an extensive region of north-western Australia. The predominantly arid character of this region (average annual rainfall <350 mm, potential evaporation 3200–4000 mm) and its largely impervious geology strongly influence the structure and function of its aquatic ecosystems (McKenzie *et al.*, 2009; Pinder *et al.*, 2010). Episodic and often cyclonic flooding characterize the intermittent and highly variable flows of the region's rivers (McKenzie *et al.*, 2009). As floods abate, rivers recede, resulting in a range of temporary to permanent river pools, many supplied by subsurface inflows and/or springs (Pinder

et al., 2010). This hydrologically intermittent and spatially structured connectedness provides dispersal pathways and promotes functional connectivity at large spatial scales (Sheldon & Thoms, 2006; Sheldon *et al.*, 2010).

A previous study of aquatic invertebrate composition in the Pilbara region (Pinder *et al.*, 2010) found little regional-scale spatial patterning, but did not account for variation in dispersal traits within the community or differences in intervening landscape between sites. Here, we re-analyse the data of Pinder *et al.* (2010) accounting for the effect of different dispersal abilities and different levels of landscape permeability to species dispersal on community structure. Functional connectivity of aquatic taxa with various dispersal capacities can be modelled using spatial networks: a lattice network can approximate dispersal of organisms moving overland (Fig. 1a), whereas a dendritic network can approximate dispersal during floods of taxa dependent on river channels (Fig. 1b) (Worthington Wilmer *et al.*, 2008; Brown & Swan, 2010; Campbell & McIntosh, 2013). However, realistic functional connectivity models of aquatic biota within arid zones should incorporate potential lateral connections between nearby rivers that occur during floods in areas of sufficiently low topography (Fig. 1c) (Walker *et al.*, 1995; Sheldon & Thoms, 2006). In addition, the availability of multiple dispersal paths in space needs to be accounted for.

Arid zone freshwater organisms can use multiple dispersal pathways: for example, species can disperse through a combination of long-distance movement along the river channels and short overland movements between nearby pools (Worthington Wilmer *et al.*, 2008), and therefore, there is a need to account for these multiple and varied dispersal strategies in seeking to explain spatial patterns in community composition. An approach to account for this diversity of dispersal paths is to model functional connectivity of aquatic invertebrates using circuit theory, which integrates over all possible movement paths weighted by the resistance to dispersal that a given organism would experience along each route (McRae, 2006; McRae *et al.*, 2008). Circuit theory is increasingly used to predict genetic connectivity between populations (Row *et al.*, 2010; Phillippsen & Lytle, 2012; Amos *et al.*, 2014), but has not yet been applied to analyse spatial patterning among riverine communities.

In this study, for each of five drainage basins, we built nine alternative models of functional connectivity. These were (1) one isolation-by-geographic distance model (IBD), which assumed straight-line connectivity between sampling sites, (2) four isolation-by-resistance models (IBR), which assumed that connectivity occurs along river channels and laterally between river channels, with varying river buffer widths representing various flood intensities and therefore distances between adjacent channels (this also accounts for differing dispersal capacities of individuals enabling them to deviate from the main river channel); and (3) four IBR models that, in addition to the above, conditioned connectivity between channels on topography, allowing higher connectivity in flat areas (to reflect temporal accumulation

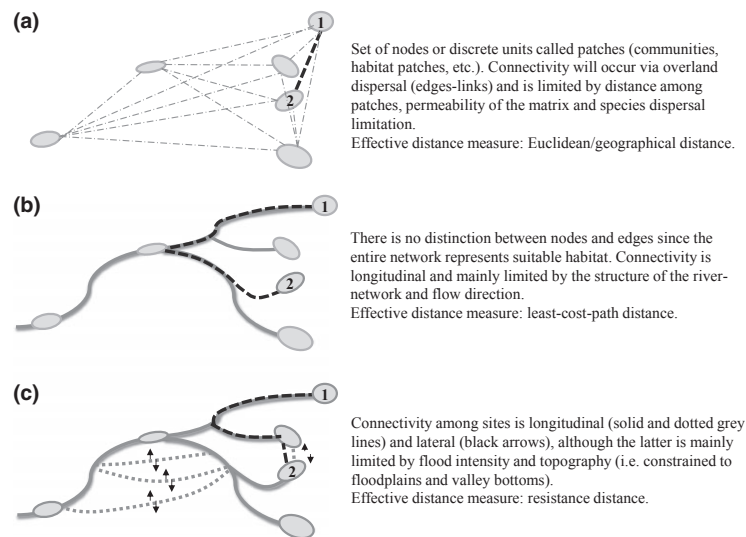


Figure 1 Types of ecological networks and corresponding measures of effective connectivity between communities. Circles and numbers represent aquatic communities (pools). The solid grey line represents the surface drainage network, and the dashed black line represents the effective distance measure between sites 1 and 2 as an example. (a) Lattice network and geographic distance; (b) dendritic network and least-cost-path distance; (c) spatial network in arid zone rivers and resistance distance: permanent riverine pools constitute patches of suitable habitat for aquatic species. After episodic flooding, water flows across a dendritic network connecting the pools (solid grey line), in some cases through multiple stream channels (mainly in flat areas: dotted grey lines). In floodplains, lateral flow will allow connection of patches through the arid matrix (black arrows).

of water in lowlands during floods and penalize connectivity among headwaters in rugged terrain). We tested these models and also a model accounting for environmental dissimilarities among sites (ENV) using compositional dissimilarities for five subsets of the invertebrate biota defined by dispersal traits: obligate aquatics, passive aerial dispersers, animals moving by aerial phoresy, weak fliers and strong fliers.

We predict that dispersal pathways (IBR or IBD) will influence spatial patterning in community composition at both the basin and regional scales whereas environmental characteristics of sites (ENV) will only influence within basin patterns. We also predict that the degree to which these models explain community patterns will vary between dispersal traits. In particular, (1) obligate aquatics should be spatially structured by IBR with narrow buffers of lateral connectivity rather than by IBD, reflecting dispersal through river channels rather than shortest path dispersal across the landscape (Fig. 2a,b); (2) passive aerial dispersers should show spatial patterning according to IBD (Fig. 2c,d) because wind dispersal results predominantly in transport of species unconstrained by water channels; (3) phoretic aerial dispersers should reflect the patterns of their dominant hosts (i.e. weak or strong active fliers; Fig. 2e,f); (4) weak aerial dispersers could show patterns consistent with IBR with wide buffers of lateral movement, reflecting movement along river channels and only short distances across the hostile terrestrial matrix (Fig. 2g,h) (Bilton *et al.*, 2001; Vanschoenwinkel *et al.*, 2009), and (5) for strong fliers, no major spatial patterning of community dissimilarities is expected (Fig. 2i,j), due to the capacity of these species to move large distances overland across the arid matrix (Brown *et al.*, 2011; Phillipsen & Lytle, 2012).

METHODS

Study region

The Pilbara region of north-western Australia covers approximately 180,000 km² and comprises five major river basins within the Indian Ocean drainage division: Onslow Coast, Fortescue River, Port Hedland Coast, De Grey River and Ashburton River (Fig. 3a). These basins (herein referred to as Onslow, Fortescue, Port Hedland, De Grey and Ashburton) have different topographic characteristics that determine the structure of their drainage networks and could influence functional connectivity (Appendix S1). Floods can connect channels within basins, primarily on the coastal plain (so mainly affecting the Onslow and Port Hedland basins), and extreme flood events can briefly connect the near coastal extents of most adjacent basins (Landgate FloodMap project, Government of Western Australia 2013, Australia; URL: <http://floodmap.landgate.wa.gov.au/>).

Invertebrate community data and calculation of community dissimilarities

We used presence–absence data for aquatic invertebrates species collected from 66 lotic sites across the Pilbara region (Fig. 3a) as part of a larger biodiversity survey (McKenzie *et al.*, 2009; Pinder *et al.*, 2010; Appendix S2). The Ashburton basin had 15 sites, De Grey had 20, Lower Fortescue had 10; Onslow had 6 and Port Hedland had 15. Lentic habitats with no connection to the river network (e.g. isolated springs) were excluded because our focus was on connectivity associated

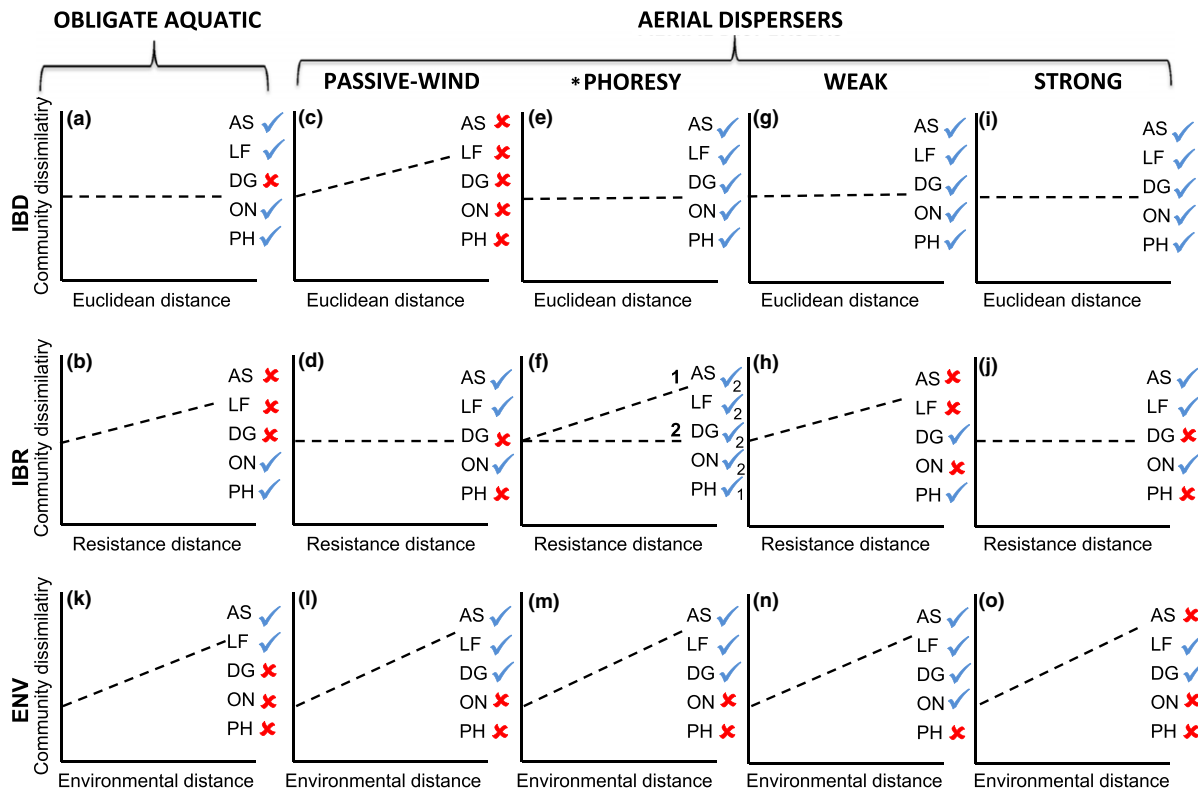


Figure 2 Predictions of distance–decay relationships (community dissimilarity vs. distance, resistance or environmental distance) for invertebrates in different arid zone dispersal trait groups (obligate aquatic, aerial passive – wind, aerial phoretic, weak active aerial and strong active aerial dispersers) at the basin scale. Isolation-by-distance models (IBD; top panels) test for community structure according to straight-line geographic distance (Euclidean distance). Isolation-by-resistance models (IBR; middle panels) test for community structure according to landscape resistance to species dispersal based on the spatial distribution of the hydrological network (river distances accounting for both longitudinal and lateral connectivity). Isolation-by-environment models (ENV; bottom panel) test for community structure according to environmental similarities (environmental distance). Prediction of lack of community structure for a given dispersal trait group and connectivity model is indicated with a horizontal line; prediction of increase in community dissimilarity with geographic distance, resistance distance or environmental distance by line with a positive slope (for simplicity we have depicted relationships as linear, but nonlinear responses are equally possible). Results of the tests of these predictions are shown in each panel as ticks (if prediction was supported) or crosses (if prediction was not supported) for five basins (two-letter abbreviations: AS- Ashburton, LF- Lower Fortescue, DG- De Grey, ON- Onslow, PH- Port Hedland). *For phoretic aerial dispersers, two distance–decay relationships can be expected, depending on whether the species are predominantly transported by weak aerial dispersers (1) or strong aerial dispersers (2).

with riverine flows. The Upper Fortescue catchment (UF, Fig. 3a) was excluded because it is hydrologically isolated from the Lower Fortescue (LF, Fig. 3a) (McKenzie *et al.*, 2009) and had too few sites to warrant separate analysis. Species records from samples collected in spring (dry season) and autumn (post-wet season) were combined for each site.

Taxa were classified into five dispersal trait groups: (1) obligate aquatic species, whose dispersal is dependent on hydrological connectivity along a watercourse. These include large crustaceans and taxa such as mussels whose larvae are parasitic on fish gills; (2) passive aerial dispersers (e.g. microcrustacea) whose propagules can be distributed by wind; (3) taxa moving by phoresy on aerial vectors (water mites); (4) aerial dispersers with weak flying abilities (e.g. mayflies) and (5) very vagile insects with strong flying abilities (e.g. dragonflies). These groupings were based on expert opinion and general

knowledge about the groups' anatomy and biology (Appendix S3 provides a description of the criteria used to classify dispersal traits and a full list of the taxa included this study). We used the *ecodist* package version 1.2.7 (Goslee & Urban, 2007) in R (R Development Core Team, 2013) to calculate a matrix of pairwise Sørensen dissimilarities (SD) between sites in each basin and across Pilbara from presence–absence data for the whole community and for each of the five trait groups. When a given dispersal group was not present at a site, that group-site combination was excluded from the analyses.

Landscape connectivity modelling

Nine landscape models were constructed to investigate the main drivers influencing the composition of each dispersal trait group. Isolation-by-distance model (IBD), accounting

for pairwise geographic distances between sites, was calculated using GeoSpatial Modelling Environment software (Beyer, 2012). Eight isolation-by-resistance (IBR) models were built using CIRCUITSCAPE (v.3.5.8; McRae, 2006; McRae *et al.*, 2008) based on the surface drainage network layer of GEOFABRIC v.2 (Australian Hydrological Geospatial Fabric, Bureau of Meteorology, Australian Government, Australia; URL: <http://www.bom.gov.au/water/geofabric/>), which represents all paths that rivers and streams take when filled with sufficient water to flow. CIRCUITSCAPE incorporates the principles of electric circuit theory and integrates dispersal through grid cells with different resistances to species movement and dispersal over all possible pathways. To model various levels of lateral connectivity (i.e. dispersal through floods of differing extents and/or different distances between river channels crossed by the dispersing organisms), we defined four sets of watercourse buffer widths (1–4) applied to both sides of each stream (Table 1).

For four simple models, IBR1_{SIMP}, IBR2_{SIMP}, IBR3_{SIMP} and IBR4_{SIMP}, all grid cells containing watercourses and their buffers were assumed to have a resistance value of 1 (equal resistance), whereas the remaining grid cells, representing intervening arid land, were assumed to have infinite resistance. As IBR1_{SIMP} represented water channel connectivity only (no overbank flooding), this can be considered an equivalent to a least-cost-path stream connectivity model.

For four topography-dependent models, IBR1_{TOPO}, IBR2_{TOPO}, IBR3_{TOPO} and IBR4_{TOPO}, resistance of grid cells containing watercourses and their buffers depended on the elevation of each grid cell as well as those of its neighbourhood (i.e. connectivity is limited by the roughness of the terrain). In particular, these models reflect limited lateral connectivity between watercourses in upland areas, moderate connectivity in areas of intermediate elevation and high connectivity on coastal floodplains. To achieve this, we calculated the topographic wetness index value of each grid cell (TWI; Moore *et al.*, 1993) on the basis of the GEODATA 9-second Digital Elevation model v.3 (Geoscience Australia, Australian Government, Australia; URL: <http://www.ga.gov.au/>); this index integrates measures of slope, flow direction and flow accumulation of each pixel, having high values in flatter areas and low values in areas with steep slopes (Fig. 3a,b; Appendix S4). We reclassified the TWI values of the river grid cells into three levels of resistance by assigning values of 1 (low resistance), 50 (mid) and 100 (high resistance) to grid cells with high, mid and low TWI values, respectively; infinite resistance values were assigned to the intervening arid environments. These resistances were chosen because they reflect understanding of arid zone river connectivity (greater landscape permeability in flatter areas and no hydrological connections between headwaters in areas of complex topography; further details on why these resistance values were selected are provided in Appendix S4). As flow direction could not be modelled, longitudinal connectivity along river channels was also penalized in areas of high topography by these models (Fig. 3b).

Finally, we calculated pairwise resistances between sampling sites within each drainage basin for all eight IBR models (see Appendix S4 for details of CIRCUITSCAPE settings). All GIS data were manipulated in ArcGIS10.1 (ESRI®).

Data on local environmental conditions

A wide range of environmental variables were measured at each site at the same time as invertebrates were sampled (see Appendix S2 for details of data collection) in spring and autumn (except four sites sampled only once after flooding events; for these, missing values were filled using data from the season sampled). We standardized the variables, removed highly correlated ones (Spearman's rank correlation >0.7) and, for each season, calculated a matrix of Euclidean distances for 22 retained variables: turbidity (nephelometric turbidity units, NTU), maximum depth of invertebrate sample (m), maximum flow (cm s⁻¹), % of submerged macrophyte cover, % of emergent macrophyte cover, conductivity (µS cm⁻¹), pH, concentrations of total filterable phosphorus (µg L⁻¹), chlorophyll (µg L⁻¹), water temperature (C), alkalinity (mg L⁻¹), silica (mg L⁻¹), nitrate (mg L⁻¹) and iron (mg L⁻¹), contribution of Na⁺, Mg²⁺, Cl⁻ and SO₄²⁻ to concentration of major ions (as percentage milliequivalents), estimated percentage of cover at the bed surface of cobble+pebble, gravel, sand and silt+clay. We refer to these models of environmental dissimilarity as ENVspr and ENVaut, for spring and autumn data, respectively.

Statistical analyses

Within each basin and trait group, we tested for correlations between pairwise Sørensen community dissimilarities (SD) and either pairwise landscape distances (IBD and IBRs) or environmental distances (ENVs) using Mantel tests (Mantel, 1967), commonly applied to address non-independence between pairwise measurements. Mantel's method tests the significance of the correlation between pairwise matrices by evaluating results from repeated randomization of their rows and columns: a *P*-value is calculated from the number of randomizations that yield a test statistic equal to or more extreme than the observed value. The Mantel statistic (*r*) is the measure of the correlation between the two matrices (correlation coefficient or effect size). Mantel tests are appropriate when hypotheses are formulated in terms of distances (Legendre & Fortin, 2010; Anderson *et al.*, 2011) and thus are suitable for testing whether community dissimilarity increases with geographic distance, landscape resistance or ecological distance. Mantel tests were performed in R using the ecodist package (Goslee & Urban, 2007; R Development Core Team, 2013) with 1000 permutations and assumed monotonic relationships were tested with Spearman's rank correlations to account for possible nonlinear relationships between variables.

For each basin, the best model of isolation-by-resistance was taken as the model with the highest significant Mantel *r*-value. If this was one of the IBR_{TOPO} models, then a partial

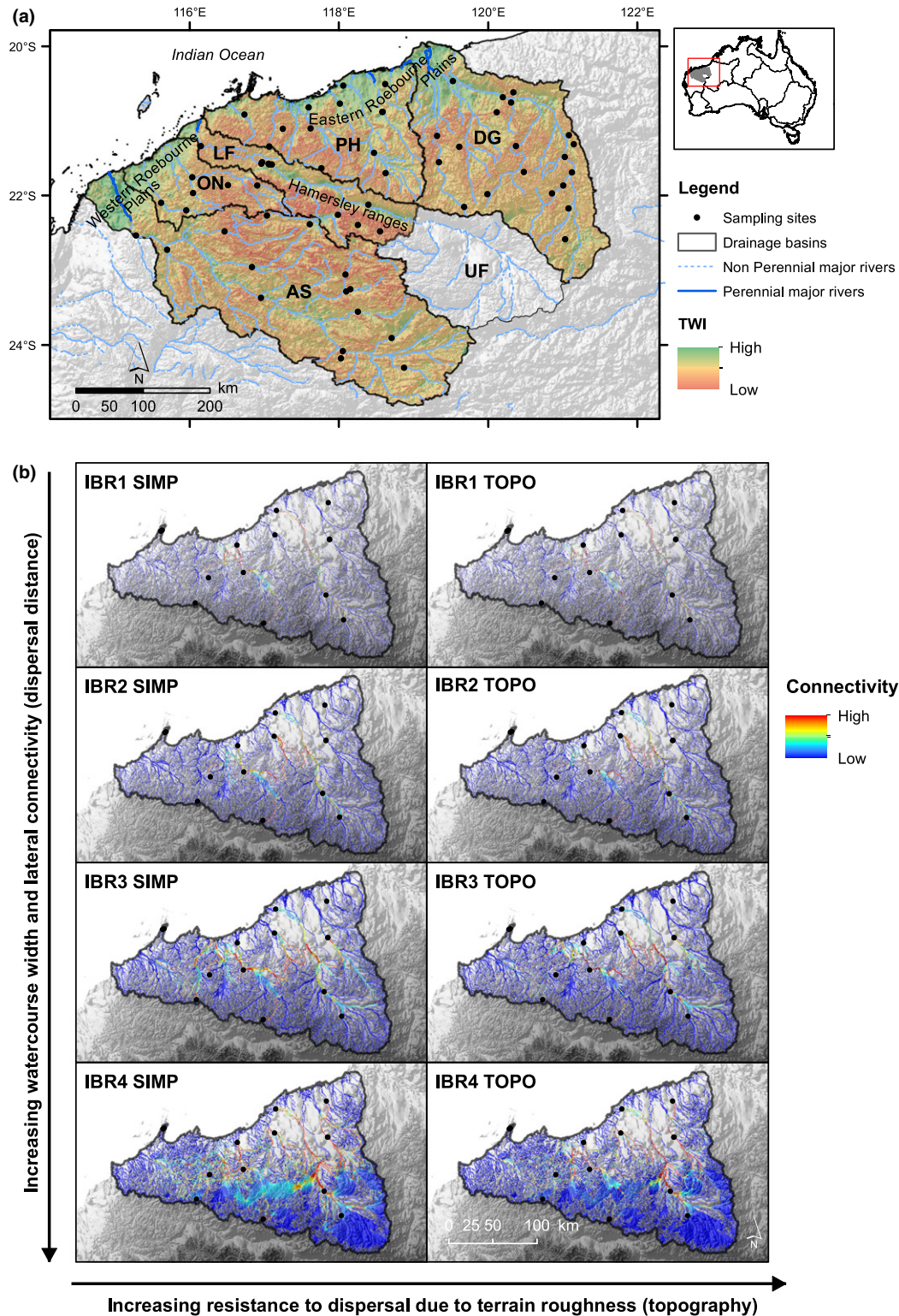
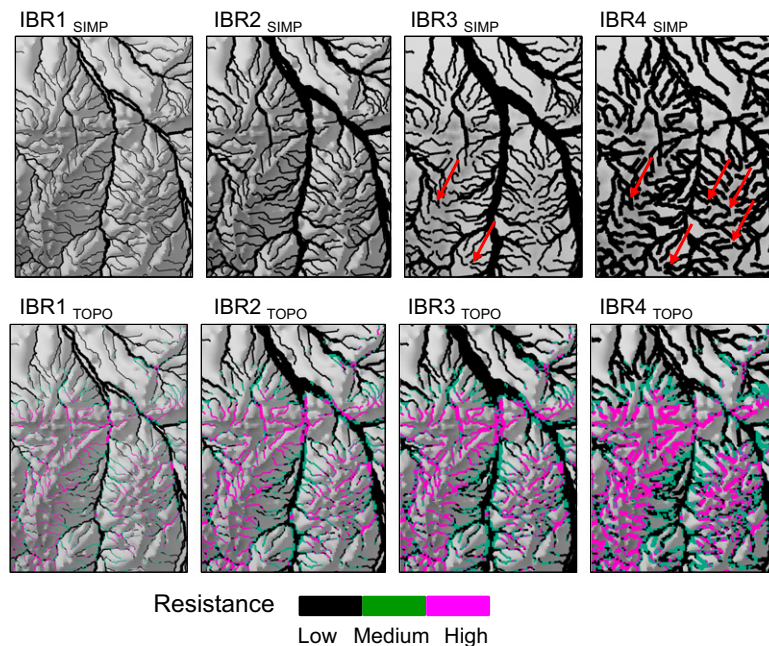


Figure 3 (a) Location of the Pilbara region (north-western Australia) and spatial distribution of sampling sites. Drainage basins are indicated with abbreviations: Onslow, (ON), Fortescue (LF and UF refer to its Lower and Upper parts, respectively), Port Hedland (PH), De Grey (DG) and Ashburton (AS). The map also shows topographic wetness index values (TWI; Moore *et al.*, 1993): higher values indicate areas of low relief, low slopes and low run-off, with high potential of water accumulation, whereas low values correspond to areas of high topographic complexity characterized by steep slopes, high run-off and therefore low water accumulation. (b) An example of eight CIRCUITSCAPE connectivity maps (called current maps) built to represent eight different isolation-by-resistance (IBR) scenarios for Port Hedland (see Table 1 for details of IBR models). The current maps highlight the most important connectivity paths across the landscape; resistance distances between pairs of sites were constructed based on these paths.

Table 1 Connectivity scenarios simulating different stream widths and levels of lateral connectivity between streams used to test community structure in the Pilbara region on the basis of resistance distance. Scenario IBR1_{SIMP} is the most realistic representation of channel width within this area, based on aerial imagery. Scenarios IBR2_{SIMP} to IBR4_{SIMP} represent increasing levels of aquatic habitat suitability and lateral connectedness. Red arrows indicate where connectivity among headwater increases when increasing the buffer widths of order 1 rivers in the different scenarios. In IBR1-4_{TOPO} (topography-dependent models), resistance of grid cells penalizes dispersal across areas of rough topography (see, for example, areas pointed out with red arrows in the maps below)

Scenario name	Width of buffer applied to stream channels (m)		
	Order 1	Orders 2 and 3	Orders 4 to 7
IBR1 _{SIMP}	50	100	200
IBR2 _{SIMP}	100	200	400
IBR3 _{SIMP}	150	300	600
IBR4 _{SIMP}	300	300	300



Mantel test was used to assess whether it explained variation in community dissimilarity after first fitting IBR_{SIMP} for the corresponding buffer width setting (Table 1); unless IBR_{TOPO} was significant on this partial Mantel test, IBR_{SIMP} was retained as the best isolation-by-resistance model. A significant ENV model with the highest Mantel *r*-value was considered the best environmental model.

When more than one model type (IBD, IBR or ENV) appeared significant on marginal Mantel tests, we used partial Mantel tests to evaluate whether each remained significant after controlling for the effect of the others (causal modelling; Legendre & Troussellier, 1988; Amos *et al.*, 2012); if a partial Mantel test was significant, the factor was considered influential in shaping invertebrate community composition. Tests were performed for each basin and also for the entire Pilbara region (in this case only IBR3_{SIMP}, IBR4_{SIMP}, IBR3_{TOPO} and IBR4_{TOPO} were tested, as they were the only IBRs allowing connection among drainage basins).

In our analyses, spatial autocorrelation of environmental variables (Nekola & White, 1999; Chase *et al.*, 2005) was accounted

for by testing the influence of geographic and resistance distances while partialling out environmental distances.

RESULTS

Ten significant relationships between community dissimilarity and landscape structure were detected in three basins across the five dispersal trait groups: De Grey, Onslow and Port Hedland (see Table 2 and Fig. 2 for a summary of inferences and Appendix S5 for Mantel *r* correlation coefficients and *P*-values of Mantel and partial Mantel tests). Nine of these relationships involved IBR models that represented moderate to high levels of lateral connectivity among streams, and one was an IBD model. IBR1_{SIMP}, approximating a least-cost-path model, was not supported for any trait group in any basin.

For obligate aquatic dispersers, we predicted that IBR models with narrow buffers would best explain community similarity within basins. However, for this trait group, IBR was correlated with community similarity only in the two

Table 2 Inferred processes shaping community composition of invertebrate aquatic species in Pilbara for each dispersal trait group and drainage basin: IBD- isolation-by-distance (geographic distances), IBR- isolation-by-resistance or ENV- environmental similarity. IBR1-4_{SIMP} refer to the four isolation-by-resistance scenarios based on the hydrological network detailed in Table 1, and IBR1-4_{TOPO} are the four isolation-by resistance scenarios that based on IBR1-4_{SIMP} models incorporate the effect of topography on the estimate of landscape resistance distances. ENV/IBR denotes cases where ENV and IBR could not be distinguished by causal modelling (see Appendix S5 for detailed Mantel R values across all 10 tested models). ‘No structure’ indicates that none of the tested alternative models correlated significantly with community dissimilarities for a given species trait group. ENVaut and ENVspr account for dissimilarities on environmental conditions based on autumn and spring samples respectively.

	Aquatic Obligate aquatic	Aerial dispersers				
		Passive (aerial)	Phoresy	Weak fliers	Strong fliers	All taxa
Predictions	IBR/ENV	IBD/ENV	IBR* or No structure [†] /ENV	IBR/ENV	ENV	
Ashburton	ENVspr	ENVaut	ENVaut	ENVaut	No structure	ENVaut
Lower Fortescue	ENVspr	ENVspr	ENVaut	ENVspr	ENVspr	ENVspr
De Grey	IBD	ENVaut/IBR4 _{TOPO}	ENVaut	ENVaut/IBR4 _{SIMP}	ENVaut/IBR4 _{TOPO}	ENVaut/IBR4 _{SIMP}
Onslow	IBR3 _{SIMP}	No structure	No structure	ENVspr	No structure	No structure
Port Hedland	IBR4 _{SIMP}	IBR4 _{SIMP}	IBR2 _{TOPO}	IBR2 _{TOPO}	IBR2 _{SIMP}	IBR2 _{SIMP}
Pilbara region	ENVaut/IBR4 _{SIMP}	ENVaut/IBR4 _{SIMP}	ENVaut	ENVspr/IBR4 _{SIMP}	ENVspr/IBR4 _{SIMP}	ENVspr/IBR4 _{SIMP}

*Prediction for phoretic aerial species predominantly transported by weak aerial dispersers.

[†]Predictions for phoretic aerial species predominantly transported by strong aerial dispersers.

basins with extensive floodplains, and these were IBR models with wide buffers; Onslow (IBR3_{SIMP}) and Port Hedland (IBR4_{SIMP}). Adding in topography did not significantly increase correlations. By contrast, in De Grey, obligate aquatic dispersers showed significant correlations only with IBD (Table 2). Passive aerial dispersers did not show the predicted relationship with IBD in any basin. Instead, IBR models with wide buffers were supported for De Grey (IBR4_{TOPO}) and Port Hedland (IBR4_{SIMP}). Composition of weak fliers, as predicted, was correlated with IBR, in De Grey (IBR4_{SIMP}) and Port Hedland (IBR2_{SIMP}). However, in contrast to our prediction, composition of strong fliers also showed correlations with IBR in the same basins (IBR2_{SIMP} for Port Hedland and IBR4_{TOPO} for De Grey). Organisms dispersing by aerial phoresy were significantly correlated with only one landscape model: IBR2_{TOPO} for Port Hedland. No landscape models were supported in Onslow for any aerial disperser group, but the small number of sites (6) may have reduced power to detect patterns. Introducing topographic penalties to connectivity increased some landscape–community correlations. In De Grey, the community structure of passive aerial dispersers and strong fliers was best explained by IBR4_{TOPO} rather than IBR4_{SIMP}. In the case of the phoresy group, IBR2_{TOPO} explained more variance within Port Hedland than the simple equivalent.

In contrast to landscape models, environmental distances (ENVaut or ENVspr) explained significant variation in community composition of all dispersal trait groups in Lower Fortescue and all except strong fliers in Ashburton. Similarly, environmental models explained a significant amount of the variation of community composition of most classes of aerial dispersers in De Grey (over and above the effects of significant landscape models depending on the dispersal group).

These results suggest that in the three larger basins where functional connectivity is most limited by topography, environmental factors exert a significant influence on community composition, whereas this was true in only one case (weak fliers in Onslow) for the two basins with extensive floodplains (Onslow and Port Hedland). Generally, at a basin scale, we observed significant correlations between composition of all dispersal trait groups combined and any of the connectivity scenarios (IBR, IBD or ENV), when at least two trait groups showed significant correlations with those corresponding scenarios (see column ‘All taxa’ in Table 2).

At the scale of the Pilbara region, environmental distances and IBR4_{SIMP} explained community dissimilarities for all trait groups (except organisms dispersing by aerial phoresy, which only showed significant correlations with environmental distances), as well as the entire community. IBD was not supported for any trait group or for the entire community at this scale (Pilbara; Table 2).

DISCUSSION

The community composition of aquatic invertebrates in the Pilbara appeared to be influenced by local environmental conditions, spatial configuration of river channels (along the dendritic network and laterally between nearby channels) or both factors. This is consistent with a previous study that suggested that there are complex interactions between local conditions and landscape factors, potentially moderated by traits (Thompson & Townsend, 2006). However, in this study, we were able to show that the relative importance of these factors in explaining community structure depended on the spatial configuration of river channels in each basin – including their immediate surrounding matrix (buffers) –

and on the dispersal traits of the constituent taxa. The importance of these factors also changed at different spatial scales (basin vs. region). Thus, local environmental conditions seem to be the primary driver of community similarity within most trait groups in the two basins that have a single long main channel with side branches (Lower Fortescue and Ashburton). In contrast, dispersal pathways – as represented by the spatial configuration of river channels – were associated with similarity of all trait-group communities in Port Hedland (a basin with areas of extensive coastal floodplains connecting channels that otherwise flow to the sea independently). In De Grey (a basin with multiple major rivers that merge only near the coast) as well as across the Pilbara region as a whole, local environmental factors and the spatial configuration and longitudinal and lateral connections of the riverine networks are needed to understand the compositional similarity of most trait groups. The advantage of testing for community structure patterns for multiple mobility groups, across different basins, at different scales and using different landscape connectivity scenarios is that we could identify patterns in individually significant results. However, we also acknowledge the potential limitations of correlative analyses such as the one presented in this study (which given the larger number of tests performed may inflate the rate of false positives).

A significant proportion of community composition for aerial dispersers was explained by the spatial configuration of the dendritic network (landscape resistance; IBR models) in two of the basins. This implies unexpected dispersal behaviour of some of the aerial dispersers groups (i.e. passive aerial and strong dispersers), suggesting that they are guided by connectivity of stream channels, perhaps due to greater moisture, food or likelihood of finding new habitat. Although hydrological connection between headwaters is unlikely in basins where headwaters are mainly located in highlands, aerial movement across headwaters appears to occur, because the model representing closest connection between headwaters (IBR4) best explained variation in community composition of most aerial dispersers in De Grey basin and passive aerial dispersers in Port Hedland (see also Fig. 3b). This suggests that aerial dispersers tend to deviate only short distances away from the river channels, but these distances are sufficient to allow occasional movement into nearby headwaters, resulting in similar communities in different river systems within the same basin. This is consistent with previous studies that suggest headwater connectivity is critical to patterning of biodiversity across river networks (Finn *et al.*, 2011).

Some aerial dispersal groups appear to be inhibited by rugged topography. In the topographically complex De Grey basin, the IBR4_{TOPO} model explained a larger amount of variance in community dissimilarity for passive dispersers and strong fliers, suggesting that rugged topography represents an obstacle for the dispersal of these two groups, with dispersal occurring principally along river channels. On the contrary, in the relatively flat Port Hedland basin, dispersal limitation

due to topographic roughness seemed not to exert any influence in the community dissimilarities of these two groups (IBR_{SIMP} models explained a larger amount of variance than IBR_{TOPO}). These differences may be the basis of genetic structuring observed along stream networks for some invertebrate groups (Finn *et al.*, 2006).

Cyclonic events, which occur on average at one to two yearly intervals in the studied region, although less frequently at a basin scale (McKenzie *et al.*, 2009), cause severe floods that affect aquatic connectivity in two complementary ways. Firstly, they refill stream channels and therefore re-establish longitudinal connectivity among pools isolated during long dry periods. This process will be common for streams, consistent with hypotheses we made supporting IBR rather than IBD models for obligate aquatic species in the Onslow and Port Hedland basins. Secondly, overbank flows create lateral connectivity between otherwise unconnected streams. This process occurs mainly on floodplains, such as the Roebourne Plains in the Onslow and Port Hedland basins, plus some smaller endorheic drainages (Fig. 3; Pinder & Leung, 2009; Landgate FloodMap project, Government of Western Australia 2013, Australia; URL: <http://floodmap.landgate.wa.gov.au/>). Contrary to our expectations, the spatial structure of obligate aquatic communities in the Onslow and Port Hedland Basin seems to be driven by this second process rather than by longitudinal connectivity along the main channels, because the models of moderate to large flooding and dispersal through lowlands were supported for this group (IBR3_{SIMP} and IBR4_{SIMP}, respectively). In Port Hedland, the IBR2 model (some lateral connectivity across the floodplain) rather than IBR1 (which is a proxy for river distances) explained dissimilarities of phoretic aerial dispersers and weak and strong fliers, suggesting that weak and strong fliers bias their flight towards riverine corridors, covering only very short distances between neighbouring streams and transporting phoretic species (mites) through their dispersal. This confirms that even dry channels represent preferred dispersal corridors for overland dispersal (e.g. through increasing likelihood of finding water, food, riverine vegetation providing shade or channelling winds; Brown & Swan, 2010; Bogan & Boersma, 2012). Whereas active fliers can select paths along river channels, connectivity of passive aerial dispersers may occur via desiccation-resistant dispersal stages being funnelled along channels by winds, or via birds moving along and close to river channels and water habitats (Bilton *et al.*, 2001; Van de Meutter *et al.*, 2006; Reynolds, 2013).

Of 25 dispersal trait group by basin combinations, 14 showed significant support for ENV models, consistent with habitat being a major driver of invertebrate community composition in dryland rivers (Sheldon *et al.*, 2002; Sheldon & Thoms, 2006; Pinder *et al.*, 2010). However, the significance of environmental conditions varied greatly among basins. Whereas environmental conditions showed no correlation with community composition in the Port Headland basin, environmental conditions did shape communities in most trait groups in Ashburton, Lower Fortescue and De Grey

basins. The Ashburton, Lower Fortescue and De Grey each consist of either a single main channel with multiple side tributaries separated by complex topography (Ashburton, Lower Fortescue) or multiple main channels that sequentially connect near the coast (De Grey). Additionally, these basins have relatively small areas of lowland floodplain compared to the Port Hedland and Onslow basins (Appendix S1). These network and topographic features may reduce dispersal potential to the extent that none of the landscape connectivity scenarios were able to explain dissimilarities between sites in Ashburton and Lower Fortescue. Where there is an absence of topographic barriers, high levels of dispersal and colonization might promote high levels of community homogenization or evenness (i.e. most of the species would show cosmopolitan distributions); in contrast, low levels of dispersal and colonization may promote community differentiation as environmental filtering may become a more important determinant of composition (Thomaz *et al.*, 2007). In the Port Hedland basin, which has extensive floodplains, environmental effects may be overridden by floods that regularly connect many of the otherwise separate channels. The De Grey river basin, which has multiple channels that connect downstream, can be thought of as somewhat intermediate between the multiple separate river channels of the Port Hedland and the long main channel network of the Ashburton and Fortescue basins. This may explain why both environmental and dispersal pathways (IBR4) were both significantly correlated with composition in this catchment. At the regional (Pilbara) scale, our results suggested that community structure is related to processes associated with local environmental conditions as well as the configuration and connectivity of riverine networks across the different basins.

Consideration of dispersal traits has increased our understanding of the ways in which spatial factors structure aquatic invertebrate communities in this arid region. This is important for the management of aquatic ecosystems and the conservation of arid zone freshwater biodiversity (Faulks *et al.*, 2010; Davis *et al.*, 2013). In contrast to the present study, Pinder *et al.* (2010) did not detect significant relationships between community composition and either geographic or least-cost-path stream distance in the Pilbara, but they did not consider dispersal capacity. Furthermore, that study included data from lotic and lentic water bodies, which likely increased the variance in composition across the dataset and could have masked spatial patterns of community structure within stream networks by including non-channel habitats. The differences in results we obtained for all taxa and for individual dispersal groups highlight the importance of analysing groups with different dispersal traits separately.

Our results showed that incorporation of lateral connectivity between streams (by specifying buffers around the river channel) into models of functional connectivity provides better models of flood and aerial connectivity than does least-cost-path (approximated here by IBR1_{SIMP}) and thus better ability to detect landscape features shaping community composition of the different dispersal groups. We note

a limitation in this approach that demands a solution: neither resistance nor least-cost-path measures account for directionally biased movement (McRae *et al.*, 2008). Flow direction is of key relevance in dendritic systems, as it plays a large role in determining dispersal rates especially for obligate aquatic species, which orientate their movement relative to flow in most cases (Brown *et al.*, 2011). Our study attempted to compensate for this limitation by considering the potential effect of topographic barriers on dispersal through the use of the topographic wetness index in the calculation of landscape resistance. However, further research is needed to incorporate hydrological constraints (e.g. flow direction, magnitude) into such models, to obtain a better understanding of landscape factors driving community structure in freshwater systems (e.g. a model of Peterson & Ver Hoef (2010) and Ver Hoef & Peterson (2010) provides a promising approach).

Our dataset is unusual because of the high degree of taxonomic resolution and the application of a standardized sampling method over a very large geographic region. While it is likely that we did not sample some rare taxa, similarity coefficients tend to be driven by species of intermediate rates of occurrence. Rare species in a dataset tend to pull most sites away from each other but not lead to significant changes in the overall patterns of relationships. As such, our data provide a strong test of the relative importance of connectivity and local conditions in driving patterns of community composition. It illustrates that the role of dispersal limitation and local species sorting are strongly dependent on both the physical context in which those processes are operating and the components of the biotic community that are of interest. Optimizing conservation investments require a clear idea of the target species and their interactions with the landscape, to determine whether resources are best directed to individual sites or networks of sites.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Topographic characteristics of the drainage basins.

Appendix S2 Details of invertebrate sample collection.

Appendix S3 Classification of species into dispersal trait groups.

Appendix S4 Parameterization of landscape resistance surfaces.

Appendix S5 Mantel test results.

BIOSKETCH

Alejandra Morán-Ordóñez is a landscape ecologist whose research focuses on understanding the environmental and anthropogenic factors driving species distributions over space and time through the use of diverse analytical tools.

Authors contributions: J.D., R.T. and P.S. conceived the main ideas and all authors contributed to their development; A.Pi. collected the data; A.M-O, A.Pa and L.S. analysed the data; and A.M-O led the writing, to which all the authors contributed greatly.

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